

THE AUDOUINELLA COMPLEX (RHODOPHYTA) IN THE WESTERN SARGASSO SEA

WILLIAM J. WOELKERLING

The macroscopic vegetation of the western Sargasso Sea is known mainly from four accounts (Harvey 1852, Boergesen 1914, Winge 1923, Parr 1939) which deal almost exclusively with the genus *Sargassum*. Except for two recent papers (Carpenter 1970, Woelkerling 1972b), only isolated records of other macroscopic or epibiotic algae from this region have appeared in the literature (Collins 1917, Conover and Sieburth 1964, Farlow 1914, Hentschell 1921, Prat 1935). These reports leave a number of points to be clarified including identification to species in most cases. To date only one reference (Conover and Sieburth 1964, p. 150) to an unidentified audouinelloid alga in this region has been published.

The present study was initiated after an analysis of several samples of *Sargassum* from the western Sargasso Sea revealed the presence of numerous epiphytic audouinelloid plants. This paper incorporates data from six cruises to the Sargasso Sea by vessels of the Woods Hole Oceanographic Institution and includes a morphotaxonomic account of the audouinelloid algae found to date.

MATERIALS AND METHODS

Samples of *Sargassum* were gathered with the aid of a long-handled dip net, immediately preserved in 1:10 formalin in sea water, and brought back to shore for subsequent study. Vouchers of all collections have been prepared in the form of permanent microscopic slides (Woelkerling 1970) or as liquid preserved material in 10:1 70% ethanol in glycerine. Herbarium numbers designated WJW are those in the author's personal collections; other herbarium abbreviations follow Lanjouw and Stafleu (1964). Line

drawings have been made with the aid of a Leitz drawing head microscope attachment.

In all cases morphological data is based on plants found in the Sargasso Sea and represents, wherever possible, the results of analyses of populations rather than of isolated plants.

The taxonomic proposals of Woelkerling (1971) have been adopted during this study, including the use of older generic names in cases of possible synonymy in order to avoid making new and unnecessary nomenclatural combinations. In species descriptions, the designation L/D refers to the ratio of cell length to cell diameter.

GENERAL OBSERVATIONS

Of the six species found to date, *Colaconema infestans* (Howe et Hoyt) comb. nov. occurs in nearly all collections, and *Audouinella daviesii* (Dillwyn) Woelk., *A. hallandica* (Kylin) comb. nov., and *A. thuretii* (Bornet) Woelk. appear fairly frequently as well. *Audouinella microscopica* (Naegeli) Woelk. and *Calaconema scundata* (Lyngbye) comb. nov., in contrast, have been encountered on only several occasions.

Monosporangia occur in all species and tetrasporangia also have been found in *A. thuretii*; sex organs, however, are apparently wanting. The formation of reproductive bodies is in noteworthy contrast to the situation in *Sargassum fluitans* (Boergesen) Boergesen and *S. natans* (L) J. Meyen, the two most conspicuous algae of the Sargasso Sea, which apparently never become fertile (see, however, Parr 1939, p. 49).

The audouinelloid algae probably represent a permanent component of the Sargasso Sea flora rather than being a temporary invading element (see Woelkerling 1972b) since they frequently epiphytize *Sargassum fluitans* and *S. natans*, which are apparently endemic to this region. However, all species found to date in the Sargasso Sea are also reported from Bermuda, the Caribbean, or the North

American mainland (Boergeson 1915, 1924; Collins and Hervey 1917; Taylor 1960). It is likely that these land masses act as distribution centers; in fact several collections examined during the present study have been attached to hosts (e.g. the grass *Spartina*) from inshore areas.

In general, the morphotaxonomic conclusions reached by Woelkerling (1971) are supported by this investigation. Differences between species in which the prostrate system is dominant and those in which the erect system is dominant have become more apparent to the author as a result of the current investigation, and it appears that at least two distinct habits occur among species with multicellular prostrate systems: 1) a stoloniferous habit in which the prostrate filaments are more or less widely creeping and give rise to erect filaments at irregular intervals, and 2) a more or less caespitose habit in which the prostrate filaments are generally pseudoparenchymatously united into a disc or funiform mass which, in turn, gives rise to a number of erect filaments in close proximity to one another. In stoloniferous forms, the prostrate system usually predominates while in caespitose forms, the erect system usually predominates.

KEY TO SPECIES

1. Prostrate system normally absent; plants attached to substrate by a single basal cell which may rarely divide to form several accessory cells.
 2. Cells generally 5-10 μ long, more or less barrel-shaped, commonly isodiametric or broader than long *Audouinella microscopica*.
 2. Cells generally 10-30 μ long, more or less cylindrical, L/D usually more than 2 *Audouinella hallandica*.
1. Prostrate system present, filamentous or pseudoparenchymatous.
 3. Plants more or less stoloniform; prostrate system exceeding erect system in length; erect filaments rarely over 90 μ long and commonly unbranched *Colaconema infestans*.
 3. Plants more or less caespitose; prostrate system not exceeding erect system in length; erect filaments commonly over 200 μ long and branched.

4. Sporangia, in part at least, grouped in clusters of 3-8 in axils of lateral branches *Audouinella daviesii*.
4. Sporangia usually solitary or in pairs, not clustered in axils of lateral branches.
5. Chromoplasts distinctly stellate; prostrate system at first a parenchyma-like group of cells; sporangia commonly on short (3-5 celled) lateral branches
..... *Colaenema secundata*.
5. Chromoplasts parietal lobate; prostrate system filamentous in young stages; sporangia situated on longer lateral branches *Audouinella thuretii*.

***Audouinella daviesii* (Naegeli) Woelkerling 1971: 28, Figs. 7, 22.**

Acrochaetium daviesii (Dillwyn) Naegeli 1861: 405, Figs. 26-27. Boergesen 1924: 25, Fig. 8. 1827: 25, Fig. 15. Taylor 1960: 307.

Callithamnion daviesii (Dillwyn) Lyngbye 1819: 129 (only as to binomial).

Ceramium daviesii (Dillwyn) C. Agardh 1817: XXVII.

Chantransia daviesii (Dillwyn) Thuret in Le Jolis 1863: 106. Kylin 1907: 117, Fig. 27. Rosenvinge 1909: 104, Fig. 34.

Conferva daviesii Dillwyn 1809: 73, Suppl. pl. F.

Rhodochorton daviesii (Dillwyn) Drew 1928: 172. Nakamura 1944: 106, Fig. 5.

Trentepohlia daviesii (Dillwyn) Areschoug 1847: 338.

Note: Further synonymy is given by Woelkerling (1971, p. 28).

Plants epiphytic or epizoic, caespitose, up to 5 mm. tall; original spore non-persistent. Prostrate system consisting of branched filaments more or less forming a pseudoparenchymatous disc. Erect filaments freely and irregularly branched, commonly attenuate and ending in multicellular hair-like prolongations. Cells of main axes and laterals cylindrical, 8-15 μ wide and (15-) 20-60 μ long, L/D (1.75-) 2-4(-5); cells sometimes tapering to 2-8 μ wide and 20-80 μ long (L/D up to 35) near the apices; each cell containing a parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, 8-13 μ wide and 13-17(-22) μ long, in clusters of 3-8 on branched stalks or singly or in pairs on 1-2 celled stalks, situated on the lowermost cells of laterals or sometimes more scattered.

Other reproductive structures not observed in material examined.

Type Locality. — Bantry Bay, Ireland (Hutchens); locality for H. Davies collection not given by Dillwyn (1809).

Holotype. — NMW.

Distribution. — Nearly cosmopolitan.

Hosts. — Hydroids, *Sargassum*, and *Spartina* (Angiospermae) fragment in Sargasso Sea; a wide variety of algae, marine angiosperms, and invertebrates elsewhere.

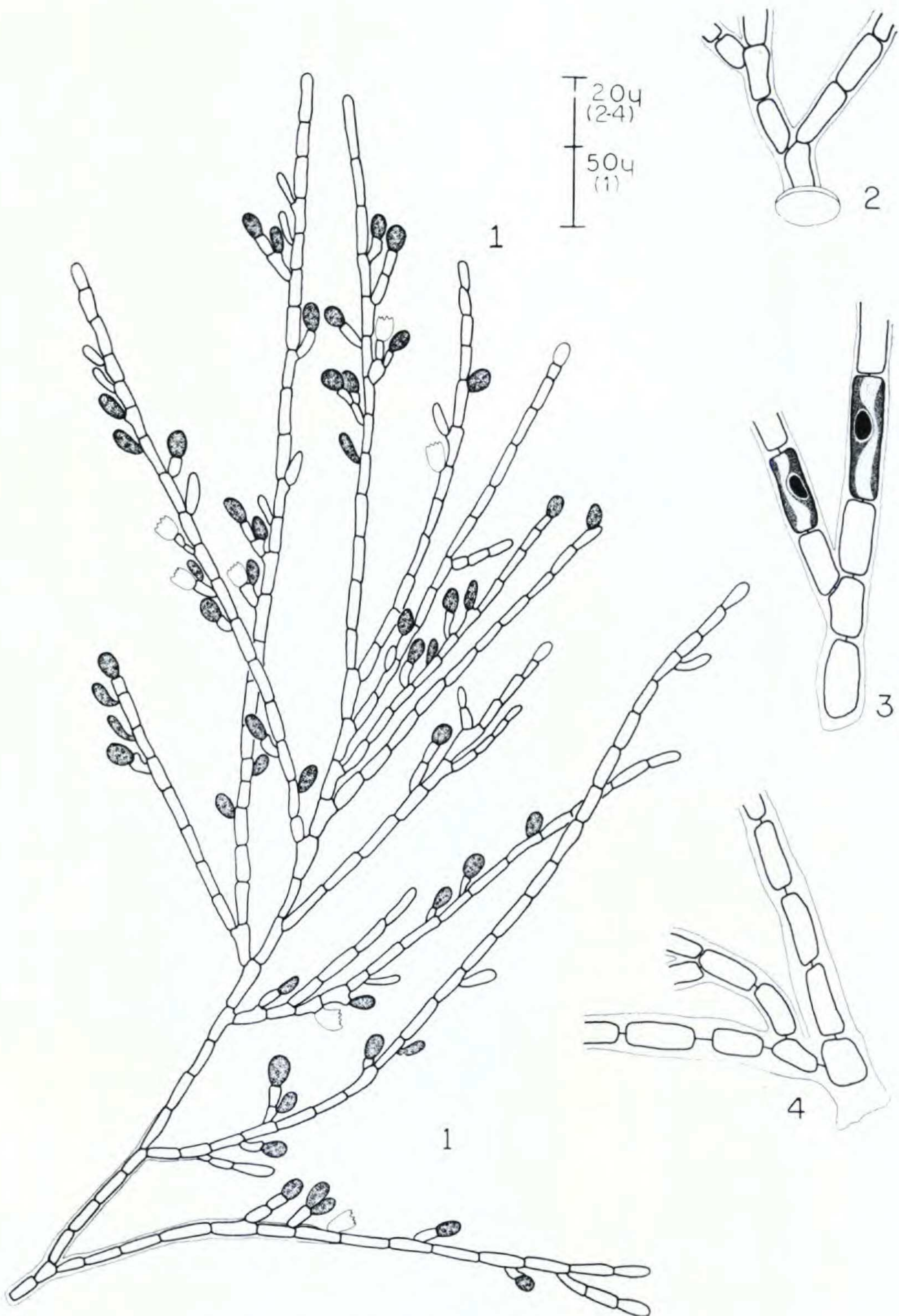
Specimens examined. — **Sargasso Sea:** 26° 57'N-72° 58'W, 26.iv.1970, Moore (WJW 2648); 28°N-70°W, 4.iii.1970, Volkman (WJW 2429); 31°N-69° 29'W, 3.iii.1970, Volkman (WJW 2380), (WJW 2364); 32° 09'N-64° 58'W, 16.V.1970, Woelkerling (WJW 2667); 34°N-70°W, 7.iii.1970, Volkman (WJW 2396), (WJW 2409); 37°N-70°W, 12.v.1970, Woelkerling (WJW 2621); 38° 22'N-70°58'W, 12.x.1970, Volkman (WJW 2888); 39° 07'N-70° 35'W, 16.viii.1970, Moore (WJW 2930). **Ireland:** Bantry Bay, prior to 1809, Hutchins (NMW, Dillwyn Collection, type).

Populations of *A. daviesii* examined during this study agree in all essentials with the type material and with plants described in the accounts of Rosenvinge (1909) and Woelkerling (1971). Multicellular hair-like prolongations with poorly developed plastids often devoid of pyrenoids occur very frequently in Sargasso Sea plants.

Clustered monosporangia are common in most collections (2621 represents the only exception), but tetrasporangial and sexual individuals (see Woelkerling 1971 for accounts of these stages) have not been encountered.

Audouinella hallandica (Kylin) comb. nov. Figs. 1-4.

Acrochaetium hallandicum (Kylin) Hamel 1927: 20, Figs. 19-21; 1928: 114, Figs. 19-21.



Figs. 1-4. *Audouinella hallandica* (Kylin) comb. nov. Fig. 1. Monosporangial plant. Figs. 2-4. Variation in shape of basal cell. Note chromoplasts (Fig. 3).

- Chantransia hallandica* Kylin 1906: 123, Fig. 8. Rosen-
vinge 1909: 93, Figs. 21-23.
- Chromastrum hallandicum* (Kylin) Papenfuss 1945: 321.
- Kylinia hallandica* (Kylin) Kylin 1944: 13, 15, Fig. 7.
- Rhodochorton hallandicum* (Kylin) Rosenvinge 1935: 7.
- Acrochaetium dufourii* (Collins) Boergesen 1915: 19.
Hoyt 1920: 470, Fig. 26. Collins *In* Collins, Holden,
and Setchell 1909: 1594 (Nom. Nud.). Collins and
Hervey 1917: 96. Taylor 1960: 305.
- Chantransia dufourii* Collins 1911: 187.
- Kylinia dufourii* (Collins) Kylin 1944: 13.
- Acrochaetium sargassi* Boergesen 1915: 17, Figs. 7-10.
Taylor 1925: 129. 1928: 134, pl. 22, Figs. 1-5. 1960:
306.
- Chantransia sargassi* (Boergesen) DeToni 1924: 45.
- Kylinia sargassi* (Boergesen) Kylin 1944: 13.

Plants epiphytic, up to 1 mm. tall, original spore per-
sisting as a unicellular base the same size or somewhat
larger than other cells and giving rise to 1-2 main axes.
Erect filaments moderately and irregularly branched, occa-
sionally tapering towards the tips; unicellular hairs not
observed. Cells cylindrical, 4-7 μ wide and 10-30 μ long (L/D
2-5), each containing a parietal lobate chromoplast and one
pyrenoid.

Monosporangia ovoid, 6-8 μ wide and 8-11 (-15) μ long,
singly or in pairs, sessile or stalked, scattered over the
erect filaments adaxially and occasionally abaxially as well.

Other reproductive structures not observed.

Type Locality. — Hogardsgrund, Halland, Sweden.

Holotype. — Apparently not designated by Kylin. Ma-
terial on three prepared slides in LD dated 13.vii.1904
has been chosen as lectotype.

Distribution. — Sargasso Sea; Europe, Atlantic Coast
of North America.

Hosts. — *Sargassum natans*, *Sargassum* sp., and hy-
droids in Sargasso Sea; elsewhere on a variety of
algae.

Specimens examined. — Sargasso Sea: 31°N-69° 29'W, 3.iii.1970, Volkmann (WJW 2385); 34°N-70°W, 10.i.1970, Volkmann (WJW 2210), 7.iii.1970, Volkmann (WJW 2401); 36°N-70° 36'W, 9.xii.1970, Moore (WJW 2944). Sweden: Hogardsgrund, Halland Coast, 13.vi.1904, Kylin (LD, lectotype). United States: Beaufort, North Carolina, 13.vii.1908, Hoyt (FH, Co-type of *Acrochaetium dufourii* Collins). Virgin Islands: St. Thomas harbour, 26.xii.1905, Boergesen (C, type of *Acrochaetium sargassi* Boergesen).

Specimens of *Audouinella hallandica* from the Sargasso Sea compare favorably with lectotype material from the Halland Coast of Sweden. Neither the lectotype nor any Sargasso Sea collections contain sexual plants; these, however, have been described from Denmark (Rosenvinge 1909, p. 93, Figs. 21-22), France (Hamel 1927, p. 20, Figs. 19-20), and the Virgin Islands (Boergesen 1915, p. 17, Figs. 7-10 — as *Acrochaetium sargassi*).

The taxa originally described as *Acrochaetium sargassi* Boergesen and *Chantransia dufourii* Collins are here considered conspecific with *Audouinella hallandica* after critical comparisons of type collection material. Plants in all three type collections show virtually the same range of cell and spore dimensions and also show good morphological agreement in other respects. Taylor (1960, p. 302) has attempted to distinguish *Acrochaetium sargassi* from *A. dufourii* on the basis of slight differences in cell width and basal cell size, but neither of these characters has proven reliable as a result of this study. Boergesen (1915, p. 19) also expressed some doubt about the taxonomic differences between the two taxa.

The morphotaxonomic relationships of *Audouinella hallandica* to other audouinelloid algae appear to be very complex and involve at least 15 other taxa (including *Chantransia parvula*, regarded by Rosenvinge (1909) and Hamel (1927) as conspecific with *Audouinella hallandica*). Pending critical studies of the types and other collections of all taxa involved, the relationships of *A. hallandica* to other species in the complex necessarily remain uncertain.

- Audouinella microscopica** (Naegeli) Woelkerling 1971: 33, Figs. 10, 23A; 1972a: 85, Figs. 1-14.
- Acrochaetium microscopicum* (Naegeli in Kuetzing) Naegeli 1861: 407, Figs. 24-25.
- Callithamnion microscopicum* Naegeli in Kuetzing 1849: 640.
- Chantransia microscopica* (Naegeli in Kuetzing) Batters in Schiffner 1916: 136, Figs. 13-18.
- Chromastrum microscopicum* (Naegeli in Kuetzing) Papenfuss 1945: 322.
- Kylinia microscopica* (Naegeli in Kuetzing) Kylin 1944: 13. Papenfuss 1947: 437.
- Rhodochorton microscopicum* (Naegeli in Kuetzing) Drew 1928: 151, 163.
- Acrochaetium catenulatum* Howe 1914: 84, pl. 31, Figs. 12-18.
- Chantransia catenulata* (Howe) DeToni 1924: 44.
- Kylinia catenulata* (Howe) Kylin 1944: 13.
- Rhodochorton catenulatum* (Howe) Nakamura 1941: 273, 280, Fig. 1.
- Acrochaetium collopodum* (Rosenvinge) Hamel 1927: 81.
- Chantransia collopoda* (Rosenvinge) Rosenvinge 1909: 81.
- Chromastrum collopodum* (Rosenvinge) Papenfuss 1945: 320.
- Kylinia collopoda* (Rosenvinge) Kylin 1944: 13, 15, Fig. 6.
- Acrochaetium compactum* Jao 1936: 241, pl. 10, Figs. 6-14.
- Chromastrum compactum* (Jao) Papenfuss 1945: 321.
- Kylinia compacta* Papenfuss 1947: 436.
- Acrochaetium crassipes* (Boergesen) Boergesen 1915: 20, Figs. 11-13. Boergesen 1927: 12, Fig. 5. Collins and Hervey 1917: 96. Howe 1918: 511. Taylor 1941: 75.
- Chantransia crassipes* Boergesen 1909: 1, Fig. 1. Taylor 1928: 134, pl. 28, Fig. 16.

Chromastrum crassipes (Boergesen) Papenfuss 1945: 321.

Kylinia crassipes (Boergesen) Kylin 1944: 13. Taylor 1960: 300.

Acrochaetium microfilum Jao 1936: 240, pl. 10, Figs. 1-5. (Non *A. microfilum* Levring 1945: 12, Fig. 4. = *A. Levringii* Papenfuss 1947: 436).

Acrochaetium moniliforme (Rosenvinge) Boergesen 1915: 22.

Chantransia moniliformis Rosenvinge 1909: 99, Figs. 28-29.

Chromastrum moniliforme (Rosenvinge) Papenfuss 1945: 322.

Kylinia moniliformis (Rosenvinge) Kylin 1944: 13.

Rhodochorton moniliforme (Rosenvinge) Drew 1928: 151, 164.

Plants epiphytic or epizoic, up to 75μ tall; original spore persisting as a unicellular base slightly smaller to slightly larger than other cells. Filaments of erect system 1-3, commonly accurate, simple or with a few secundly to irregularly arranged laterals. Cells barrel shaped to cylindrical, $5-9\mu$ wide and $5-10\mu$ long (L/D .75-2); each cell containing a parietal irregularly lobate chromoplast with one pyrenoid. Unicellular hairs up to 75μ long occur.

Monosporangia ovoid, $4-7\mu$ wide and $5-8\mu$ long, terminal or lateral, single or rarely in pairs, sessile or stalked, adaxially seriate or occasionally more scattered.

Other reproductive structures not observed.

Type Locality. — Torquay, England.

Holotype. — L, No. 940285 . . . 306.

Distribution. — Nearly cosmopolitan.

Hosts. — *Dictyota*, *Sphacelaria*, and hydroids in Sargasso Sea; a wide variety of algae elsewhere.

Specimens examined. — Sargasso Sea: $32^{\circ} 09'N-60^{\circ} 58'W$, 16.v. 1970, Woelkerling (WJW 3232); $34^{\circ}N-70^{\circ}W$, 10.i.1970, Volkmann (WJW 2215), 7.iii.1970, Volkmann (WJW 2408). England: Torquay, 1845, Naegeli (L 940285 . . . 306, type).

Two of the three Sargasso Sea collections (WJW 2215, WJW 2408) contain only several plants each of *A. microscopica*. The other collection (3232) contains numerous plants on a fragment of *Dictyota* collected about 14 km. off Bermuda; it seems likely that the host had drifted out from shore. The apparent rarity of *A. microscopica* in the western Sargasso Sea suggests that it may not be a permanent component of the flora.

Woelkerling (1972a) has recently presented a detailed account of this species including descriptions of sexual stages and has reduced to synonymy of a number of allied taxa cited as references in this account.

Audouinella thuretii (Bornet) Woelkerling 1971: 36, Figs. 12, 24.

Acrochaetium thuretii (Bornet) Collins et Hervey 1917: 98. Taylor 1960: 310.

Chantransia thuretii Bornet. Collins 1900: 49 (Nom. Nud.)

Chantransia thuretii (Bornet) Kylin 1907: 119, Fig. 28.

Rhodochorton thuretii Drew 1928: 171.

Chantransia corymbifera Thuret in LeJolis 1863: 107 (in part; see Papenfuss 1945: 313 under *Acrochaetium bornetii*).

Chantrancia efflorescens var *thuretii* Bornet 1904: XVI, pl. 1. Collins 1906: 196.

Plants epiphytic, caespitose, up to 5 mm. tall; original spore nonpersistent. Prostrate system consisting of branched filaments more or less forming a pseudoparenchymatous disc. Erect filaments freely and irregularly branched and sometimes tapering towards the tips; unicellular hairs not present. Cells of main axes and laterals 8-12(-16) μ wide and 20-80 μ long (L/D (2-)3-5(-8)), sometimes tapering to 4-7 μ wide near the apices; each cell containing a parietal lobate chromoplast and one pyrenoid.

Monosporangia ovoid, 8-12 μ wide and 16-24 μ long, solitary or occasionally in pairs, sessile or sometimes stalked,

generally situated adaxially on the lower portions of lateral branches but occasionally more scattered and/or terminal. Tetrasporangia ovoid to globose, 16-24 μ wide and 20-30 μ long, solitary or occasionally in pairs, sessile or occasionally stalked, scattered over laterals and main axes.

Other reproductive structures not observed.

Type Locality. — Cherbourg, France.

Holotype. — PC.

Distribution. — Nearly cosmopolitan.

Hosts. — *Sargassum natans* and *Sargassum* sp. in Sargasso Sea; elsewhere on a variety of algae and marine angiosperms.

Specimens examined. — Sargasso Sea: 28°N-70°W, 4.iii.1970, Volkman (WJW 2424); 31°N-69° 29'W, 3.iii.1970, Volkman (WJW 2379); 33° 58.5'N-69° 56.5'W, 15.v.1970, Woelkerling (WJW 2592); 34°N-70°W, 10.i.1970, Volkman (WJW 2203); 36°N-70° 36'W, 9.xii.1970, Moore (WJW 2934), (WJW 2943); 37°N-70°W, 12.v.1970, Woelkerling (WJW 3221); 38° 22'N-70° 58'W, 12.x.1970, Volkman (WJW 2889).

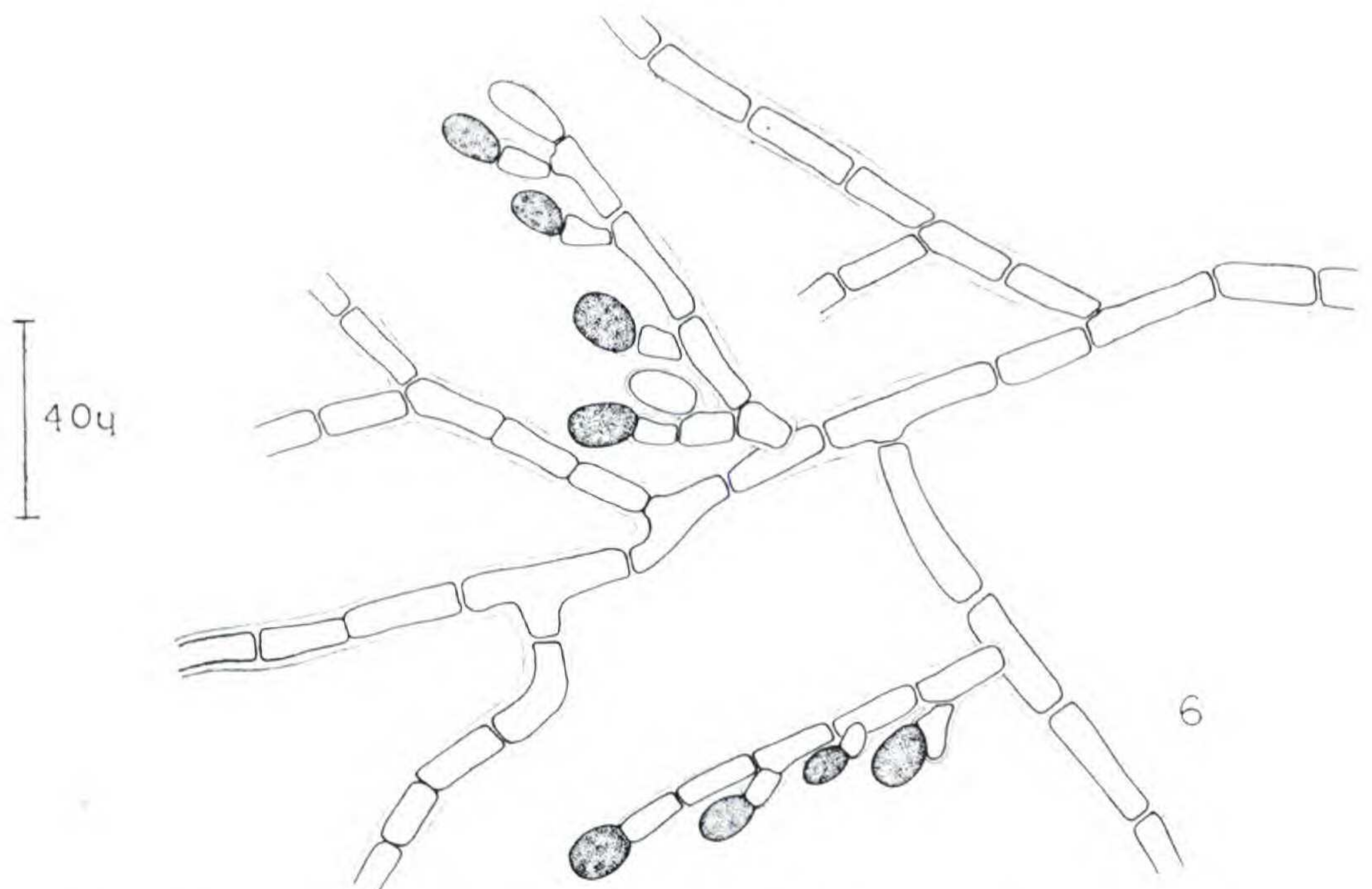
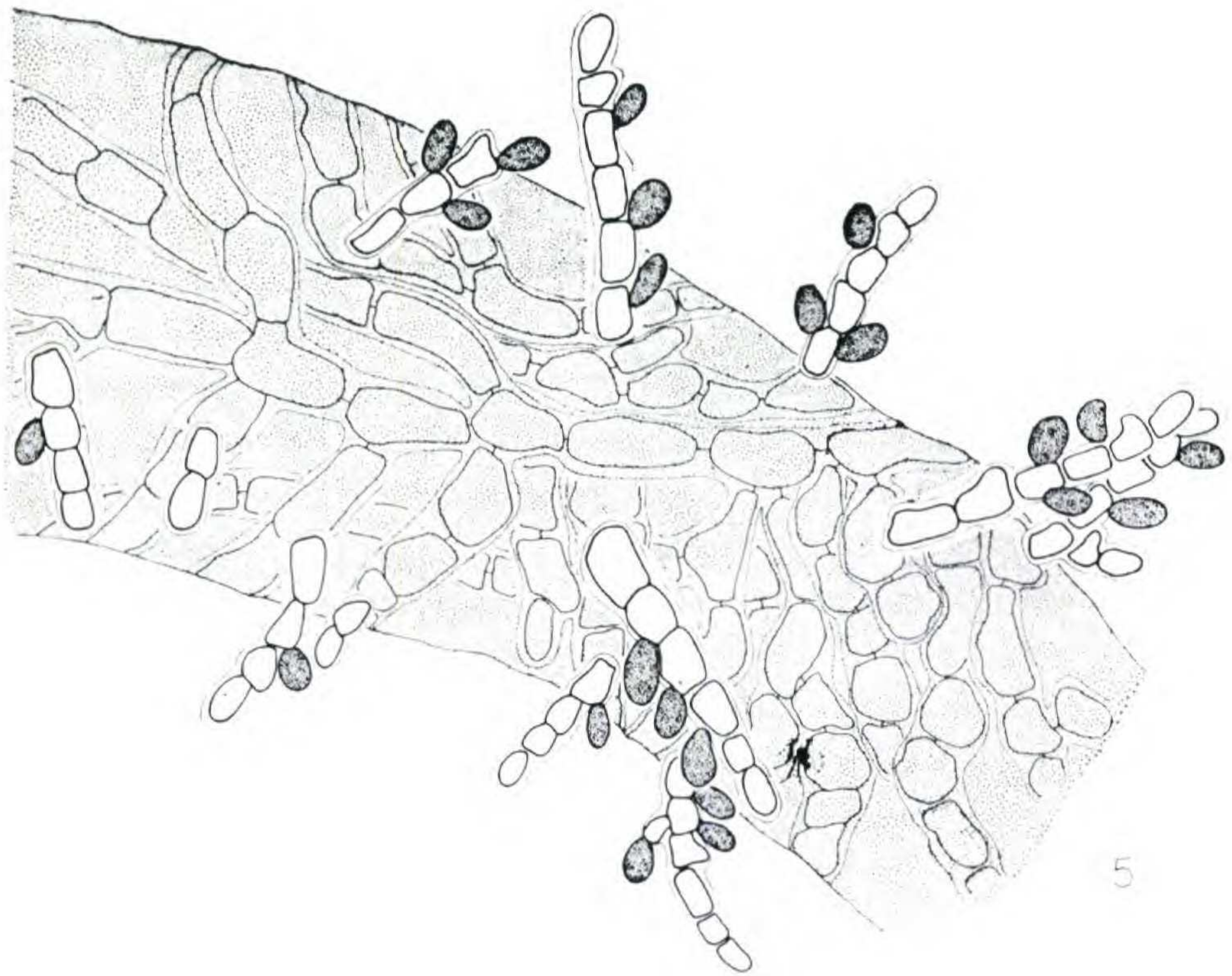
Specimens of *Audouinella thuretii* agree in general with descriptions of Rosenvinge (1909) and Woelkerling (1971). Sexual plants are described in detail by Kylin (1907).

The relationship of *A. thuretii* to other audouinelloid algae requires further investigation. Two similar species — *Acrochaetium avrainvillae* Boergesen (see Boergesen 1915, p. 48, Figs. 47-49) and *A. Nematlonis* (DeNotaris) Bornet (see Collins and Hervey 1917, p. 98; Taylor 1960, p. 314) — occur in the Sargasso Sea region (Virgin Is. and Bermuda, respectively), but until the types and other collections of all three taxa can be compared, they are best maintained as distinct species. The major difference between *A. Nematlonis* and the Sargasso Sea specimens of *Audouinella thuretii* is apparently the lack of a funiform prostrate system in the latter, and this difference is of dubious taxonomic value (Woelkerling 1971).

Colaonema infestans (Howe et Hoyt) comb. nov. Figs. 5-6.

Acrochaetium infestans Howe et Hoyt 1916: 116, pl. 14.

Howe 1918: 511. Hoyt 1920: 473, pl. CXVIII.



Figs. 5-6. *Colaonema infestans* (Howe et Hoyt) comb. nov.
Habit of monosporangial plant (Shaded portion represents host).

Chantransia infestans (Howe et Hoyt) DeToni 1924: 64.

Chromastrum infestans (Howe et Hoyt) Papenfuss
1945: 324.

Kylinia infestans (Howe et Hoyt) Papenfuss 1947: 438.
Taylor 1960: 301.

Rhodochorton infestans (Howe et Hoyt) Drew 1928:
151, 187. Nakamura 1944: 118, Fig. 13.

Rhodochorton membranaceum auct. non. (Magnus)
Hauck: Collins and Hervey 1917: 148.

Plants partly endozoic, more or less stoloniform, up 90μ tall, exclusive of hairs. Prostrate system consisting of branched, stoloniferous filaments creeping just beneath the surface of the host, sometimes becoming very congested and appearing pseudoparenchymatous; cells cylindrical to irregular in shape, $4-6(-10)\mu$ wide and $5-40\mu$ long (L/D 1-8). Erect filaments arising more or less perpendicularly from the prostrate system, simple or sparingly and irregularly branched, occasionally bearing terminal hairs up to 125μ long. Cells cylindrical, $3-7\mu$ wide and $6-30\mu$ long (L/D 2-5), each bearing a single parietal lobate chromoplast with one pyrenoid.

Monosporangia ovoid, $4-6(-8)\mu$ wide and $6-10(-15)\mu$ long, sessile or stalked, borne singly or in pairs, scattered over the erect filaments.

Other reproductive structures not observed.

Type locality. — A reef about 37km. off of Beaufort, North Carolina.

Holotype. — NY.

Distribution. — Sargasso Sea; Bermuda, Japan, North Carolina.

Hosts. — Hydroids.

Specimens examined. — Sargasso Sea: $26^{\circ} 50'N-71^{\circ} 48'W$, 5.iii.1970, Volkman (WJW 2420); $28^{\circ}N-70^{\circ}W$, 4.iii.1970, Volkman (WJW 3432); $31^{\circ}N-69^{\circ} 29'W$, 3.iii.1970, Volkman (WJW 2389); $34^{\circ}N-70^{\circ}W$, 7.iii.1970, Volkman (WJW 2403), 30.vi.1970, Volkman (WJW 2725), 6.vii.1970, Volkman (WJW 2749); $35^{\circ} 54'-70^{\circ} 30'W$, 13.viii.1970, Moore (WJW 2902); $36^{\circ}N-70^{\circ} 36'W$, 9.xii.1970, Moore (WJW 2949), (WJW 2938); $36^{\circ} 28'N-70^{\circ} 29'W$, 15.viii.1970,

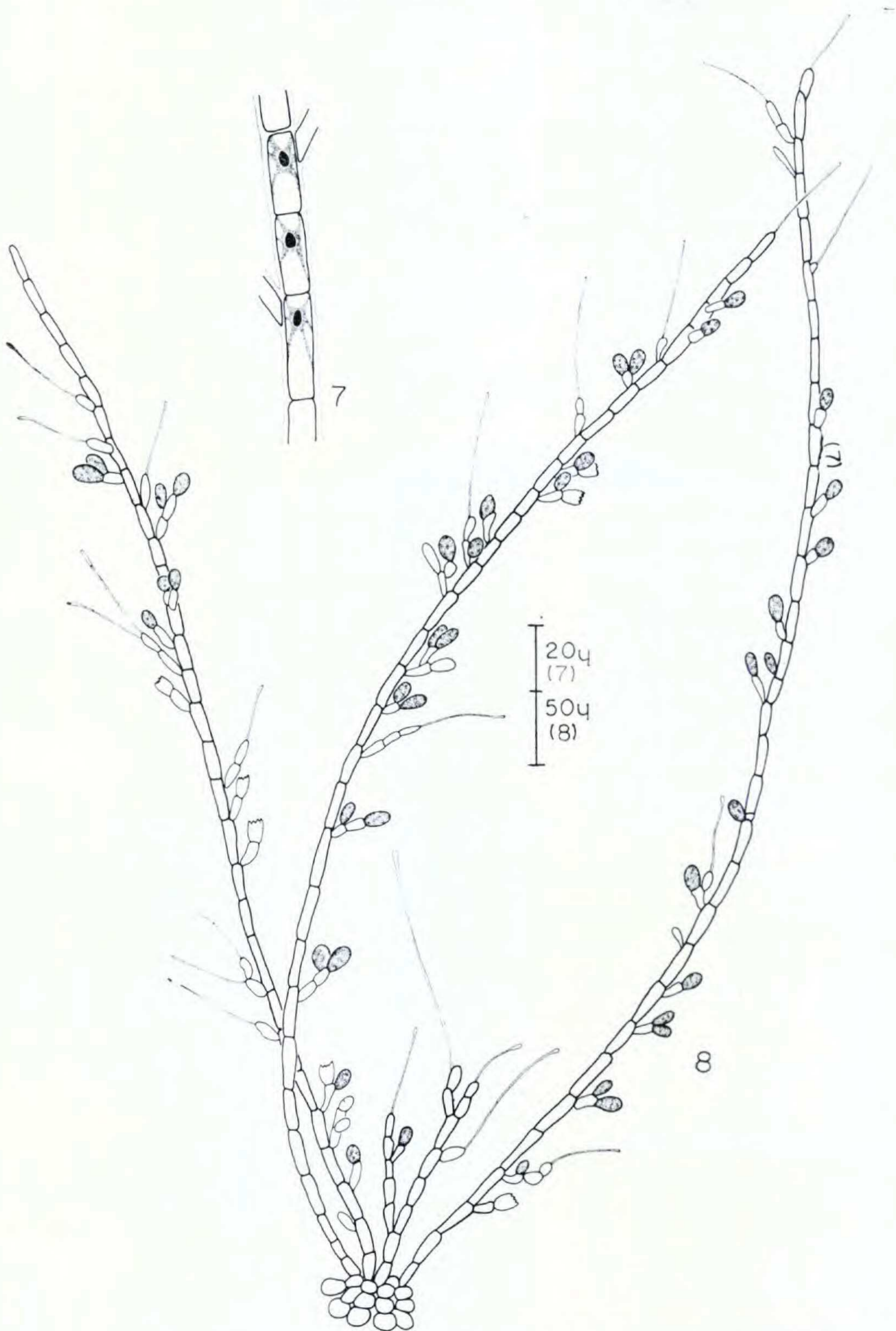
Moore (WJW 2907); 37° 30'N-70°W, 8.vii.1970, *Volkman* (WJW 2706); 38° 22'N-70° 58'W, 12.x.1970, *Volkman* (WJW 2887); 39° 07'N-70° 35'W, 16.viii.1970, *Moore* (WJW 2917), (WJW 2929); 39° 30'N-71°W, 6.x.1970, *Volkman* (WJW 2810). United States: Beaufort, N. Carolina, 11.viii.1914, *Radcliffe* (NY, type).

Specimens of *Colaconema infestans* from the Sargasso Sea agree in general with the type material on a prepared slide in NY. This species occurs very commonly in the Sargasso Sea and has been found in nearly every collection of *Sargassum* bearing the hydroid hosts. Erect filaments rarely exceed 10 cells in length, and laterals normally do not exceed four cells in length.

The relationships of *C. infestans* to a number of other audouinelloid algae of similar morphology requires clarification. *Acrochaetium effusum* Levring 1953, p. 479, Figs. 13F-G and *Rhodochorton penetrans* Drew 1928, p. 187, pl. 44, Figs. 57-58, pl. 45, Figs. 59-60 do not appear to differ significantly from *Colaconema infestans* and a comparison of the types will probably show the three taxa to be conspecific. *Chantransia endozoica* Darbishire 1899, p. 13, pl. 1 appears to have larger cells, and further study is needed to determine whether intermediate forms occur. Pending the results of such investigation, *C. endozoica* and *Colaconema infestans* are maintained as distinct species.

The relationships of *Colaconema infestans* to a number of adouinelloid taxa growing on plant hosts also requires clarification, especially since host specificity does not appear to be a reliable criterion of specific distinction (Woelkerling 1971). Endophytic taxa of similar morphology include *Acrochaetium antillarum* Taylor 1942, p. 78, pl. 2, Figs. 3-4, *A. endophyticum* Batters 1896, p. 386, *Chantransia emergens* Rosenvinge 1909, p. 128, Fig. 55, and *Colaconema porphyrae* (Drew) Woelkerling (see Drew 1928, p. 188, pl. 46, Figs. 70-75; Woelkerling 1971, p. 50, Figs. 20, 27B), and critical studies on the types and other collections of these taxa may show some or all to be conspecific.

Further investigations are also needed to determine



Figs. 7-8. *Colaçonema secundata* (Lyngbye) comb. nov. Fig. 7. Chromoplasts in vegetative cells. Fig. 8. Habit of fairly small mono-sporangial plant.

whether or not *Colaconema bonnemaisoniae* Batters and related taxa (see Woelkerling 1971, p. 42) possibly represent prostrate system stages of *C. infestans*.

Specimens of Collins and Hervey (1917, p. 148) from Bermuda referred to *Rhodochorton membranaceum* (Magnus) Hauck and distributed in the PBA, Vol. XLIV, No. 2194 (Collins, Holden, and Setchell 1917) have been examined and found to be plants of *Colaconema infestans*. Howe (1918, p. 511) reached the same conclusion.

Colaconema secundata (Lyngbye) comb. nov. Figs. 7-8.

Acrochaetium secundatum (Lyngbye) Naegeli 1861: 405.

Callithamnion secundatum (Lyngbye) C. Ag. 1828: 187.

Ceramium secundatum (Lyngbye) C. Agardh 1824: 132.

Chantransia secundata (Lyngbye) Thuret *In* Le Jolis 1863: 106.

Chromastrum secundatum (Lyngbye) Papenfuss 1945: 323.

Kylinia secundata (Lyngbye) Papenfuss 1947: 437.

Callithamnion daviesii var. *secundatum* Lyngbye 1819: 129, pl. 41, Fig. B4-6.

Acrochaetium luxurians (J. Agardh) Naegeli 1861: 405.

Callithamnion luxurians J. Agardh 1851: 14.

Chantransia luxurians (J. Agardh) Kylin 1907: 117, Fig. 26.

Acrochaetium virgatulum (Harvey) Bornet 1904: XXII.

Boergesen 1927: 14, Figs. 7-8. Chapman 1963: 56.

Hoyt 1920: 473, Figs. 29-30. Taylor 1941: 75.

Callithamnion virgatulam Harvey *In* Hooker 1833: 349.

Chantransia virgatula (Harvey) Thuret *In* LeJolis 1863: 106. Rosenvinge 1909: 109, Figs. 37-41.

Chromastrum virgatulum (Harvey) Papenfuss 1945: 323.

Kylinia virgatula (Harvey) Papenfuss 1947: 437.

Rhodochorton virgatulum (Harvey) Rosenvinge 1935: 7.

Trentepohlia virgatula (Harvey) Farlow 1881: 109.

Plants epiphytic or epizoic, more or less virgate, up to 2mm. tall; original spore non-persistent. Prostrate system at first a parenchyma-like group of cells, later forming a small, more or less circular pseudoparenchymatous disc of one to several cell layers. Erect filaments nearly simple to moderately branched, commonly bearing short laterals giving plant a virgate appearance; terminal and pseudo-lateral hairs common. Cells of erect filaments cylindrical (6-) 8-12 μ wide and (10-) 20-70 μ long (L/D 1-7), each with a distinctly stellate chromoplast and one pyrenoid.

Monosporangia ovoid, (6-) 9-13 μ wide and (10-) 16-24 μ long, sessile or stalked, solitary, in pairs or occasionally in threes, commonly crowded laterally or terminally on the shorter laterals or occasionally more scattered.

Other reproductive structures not observed.

Type locality. — Kvivig, Faeroes Islands (on "*Conferva rupestris*").

Holotype. — C.

Distribution. — Sargasso Sea; Atlantic Shores of North America, Canary Islands, Europe.

Hosts. — *Sargassum fluitans*, *S. natans*, and hydroids in Sargasso Sea; a wide variety of algae elsewhere.

Specimens examined. — **Sargasso Sea:** 28°N-70°W, 4.iii.1970, *Volkmann* (WJW 2425); 31°N-69° 29'W, 3.iii.1970, *Volkmann* (WJW 2367); 39° 30'N-71°W, 6.x.1970, *Volkmann* (WJW 2865). **England:** Torquay, prior to 1833, *Griffiths* (TCD, type of *Acrochaetium virgatulum* (Harvey) Bornet). **Faeroes Islands:** Kvivig, 19.vi.1817, ? (C, Herb. Lyngbye, type). **Sweden:** Kattegat Channel, no date, ? (LD 35117, type of *Callithamnion luxurians* J. Agardh).

The few specimens of *Colaçonema secundata* from the Sargasso Sea agree well with type material from the Faeroes Islands. Although an extremely variable species, *C. secundata* can be distinguished from other audouinelloid algae by the following combination of characters (in addition to cell and spore dimensions): 1) Spore germinating to form a distinctive parenchymatous group of cells which may later proliferate (see Kylin 1907, p. 115, Fig. 24;

Rosenvinge 1909, Figs. 37-41); 2) Cells with a distinctly stellate chromoplast with a centrally located pyrenoid, and in many cases 3) sporangia densely crowded on short lateral branches and 4) numerous terminal hairs, often terminating 1-2 celled branchlets. Tetrasporangia have not been observed but are reported by Hehre and Mathieson (1970), Kylin (1907, 1944), and Rosenvinge (1909) among others. Sexual stages remain unknown.

Unicellular hairs occur very commonly in *C. secundata* and often terminate 1-2 celled lateral branchlets, thus appearing stalked (Fig. 8).

In agreement with Hamel (1927, 1928) and Rosenvinge (1909), the taxa originally described as *Callithamnion luxurians* J. Agardh (1851, p. 14) and *C. virgatula* Harvey In Hooker (1833, p. 349) are considered conspecific with *Colaconema secundata*. The type collections of all three have been examined during this study and found to agree in all essential features. Since the specific epithet "secundata", first used by C. Agardh (1824, p. 132), predates the specific epithet "virgatula" (Harvey 1833) used by Hamel (1927, 1928) and Rosenvinge (1909) by nine years, it has nomenclatural priority.

Some authors (e.g. Kylin 1944, Taylor 1957) have maintained *C. secundata* and *Callithamnion* (= *Acrochaetium*, *Kylinia*) *virgatula* as distinct species on the bases of differences in the number of layers in the prostrate system or on slight differences in height, branching, or cell size, but as noted by Rosenvinge (1909), and as observed in New England collections (Woelkerling, unpublished data), considerable variation occurs in all cases, and species limits between the two taxa cannot be drawn reliably.

The taxonomy and relationships of *Colaconema secundata* to other taxa are quite involved and will be dealt with at a later date.

SUMMARY

The *Audouinella* complex is represented in the Western

Sargasso Sea by four species of *Audouinella* and two species of *Colaconema*, all newly recorded for this region. These species apparently constitute a permanent component of the Sargasso Sea flora, reproducing asexually by monospores and/or tetraspores. Species with a stoloniferous habit tend to produce more extensive prostrate systems than erect systems, whereas caespitose species usually possess better developed erect systems than prostrate systems. Critical comparisons of type and other collections indicate that *Acrochaetium dufourii* (Collins) Boergesen and *A. sargassi* Boergesen are conspecific with *Audouinella hallowellii* (Kylin) comb. nov., and *Acrochaetium luxurians* (J. Agardh) Naegeli and *A. virgatula* (Harvey) Bornet are conspecific with *Colaconema secundata* (Lyngbye) comb. nov. Detailed descriptions of Sargasso Sea collections together with a taxonomic key are provided.

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DEPARTMENT OF BOTANY
UNIVERSITY OF WISCONSIN
MADISON, WISCONSIN 53706